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FURTHER NOTES ON THE MECHANICAL GENESIS OF TOOTH-FORMS.

BY J. A. RYDER.

In a paper published in the Proceedings of the Academy of Natural Sciences of Philadelphia,[1] in 1878, I sought to indicate the modes in which the teeth of mammals were modified by means of the movements of their jaws incident to mastication, through long series of generations. I there reached the conclusion that mechanical strains and impacts had probably been the secondary causes to which the origin of the various forms of teeth might, in large measure, be attributed. The teeth were supposed to be plastic, or at least slightly so, in all stages, notwithstanding their extreme hardness. This view was forced upon me by facts presented by vertebrate palæontology, together with my observation that the physiological act of mastication was progressively specialized, and in each case its degree of specialization was found to be in correspondence with the type of molar tooth with which it was associated. In the course of my studies it seemed clear to me that the tooth-modifying capacity resided in the powers of the animals themselves, and the ways in which they were *compelled*,[2] according to the kind of food for which they had a preference, to exert their powers. I am aware that this sort of reasoning amounts to saying that an animal causes its own structures to vary in form, by the natural operation of its own powers in overcoming resistances, which view, notwithstanding its seeming improbability, has more in its favor than that which holds that chance variations, which have been of benefit to individuals, have been preserved and transmitted to offspring and developed into organs in the course of generations by the operation of the law of natural selection, the importance of which I would be the last to underrate. The latter view gives us no causal interpretation for so-called spontaneous variations, which the view here advocated, in some cases at least, affords; though I do not wish to be understood as saying that it gives such an interpretation in a large proportion of instances where the history of the interacting modifying forces are as yet perhaps imperfectly known. Natural selection is quite adequate to account for the development of an organ, or part, after it has made its appearance, but it leaves the initial step causally unaccounted for, which, it must be confessed, is the point where the Lamarckian hypothesis seeks to supply the needed differentiating causes. The hap-hazard, causeless variation of organisms cannot, in the nature of things, exist; it is contrary to all known precedent as exhibited in the phenomena of the inorganic world.

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[1] "On the Mechanical Genesis of Tooth-Forms," pp. 45–80.

[2] Emphatically not wholly of their own wills, because the specialization of organization presupposes a certain limitation in the power to make choice caused by habits, which have become physiological characteristics, so that the charge made against Lamarckianism that it throws all outside power out of consideration, no matter of what character, is utterly false on scientific grounds alone.

In studying the teeth, one is confronted by a number of large series of forms which clearly demonstrate the fact that large numbers of allied species which have succeeded each other in geological time bear a genealogical relation to each other. The earliest forms of teeth being the simplest, the later ones seem to have been derived from them by a process easily understood, if mechanically interpreted. The tooth earliest developed of all, seems to have been a simple hollow cone superimposed upon a nutrient papilla; indeed the enamel and dentinal portion seems to be developed from its superficial (epithelial) layers of cells which elongate as they grow and crowd together, becoming columnar, whilst the excessively hard salts of lime constituting the dentine aud enamel are deposited around the columnar matrix of cells or odontoblasts by secretion, leaving a fine tubular cavity in the centre, from which the odontoblasts retreat as their substance is crowded out by the formation of the hard material around them. In living teeth these are always joined to the dentine fibrils, especially in those rootless ones which are constantly growing and wearing away during the whole life-time of the animal. It is true, as an objection to my view, that the tooth is not protruded until its crown is in all respects fully developed and hardened, but it is not improbable that teeth, like bones, though apparently very hard, may be modified by strains falling upon them persistently in approximately one way for many hundreds of generations. The hardest substances are elastic, compressible, and flexible, and I think it will hardly be doubted that enamel and dentine in possessing these three qualities, though manifested in an inconceivably small degree under ordinary circumstances, may, when acted upon by forces exerted and repeated millions, perhaps billions of times in the course of generations, be effectual in transmitting the simple primary form to a more complex later one, as I have tried to show more fully in the paper already cited. That a brittle inflexible substance like marble, when in the form of thin, rectangular slabs may be bent by the force of gravity acting upon it persistently whilst lying horizontally for a long time and only supported at two of its corners diagonally opposite each other, is proved by an old marble gravestone very much bent from this cause and now belonging to the Academy. This phenomenon it seems to me is no harder to explain than the morphological phenomena presented by the teeth of mammals; for my part, I believe that both the phenomena in question will most probably bear a similar interpretation.

I now propose to offer some new evidence based upon more accurate observations of the mode in which herbivorous ungulates crush and masticate their food. A large living male rhinoceros has afforded me the opportunity to make the observations. *I distinctly saw this creature crush its food by sweeping the lower molars of the side about to be brought into action, from without inwards against the upper ones;* meanwhile those on the other side of the head were of course scarcely in contact, provided a considerable amount of food was being acted upon by the side in use at the instant. This, I concluded, for obvious reasons, was definitely the mode in which the jaws of ungulates were used which were moved in both lateral and vertical directions in the act of chewing; in other words, it seems to be the manner in which chewing is effected in all anisognathous selenodont mammals, which can be definitely traced to a bunodont ancestry.

It will be readily understood that the above observations in some measure modify the conclusions reached in my former paper, in which the belief was entertained that the motion which did the crushing was outwards instead of inwards. From facts which I have gathered, it now seems strange to me that I should have fallen into this misapprehension, since the true method promises to yield even a better interpretation of the true philosophy of tooth-modification by mechanical agencies than that first offered. It must, however, here be stated that, in no essential particular except one, do I alter my former views. I still hold the mandibular articulations to be the principal odontomorphic centres, as all mandibular movements are regulated from them as axes.

From the fact that the movements are from without inwards in selenodonts generally, the outer series of cusps, in the advent of such lateral movements, seem to be most compressed laterally and their tips most deflected in an inward direction, and I shall therefore consider the cause as acting from the outside instead of from the inside as formerly. The paleontological evidence afforded by symborodonts, where the selonodont or crescent-shaped cusp first appears in the outer row of molar cusps, whilst the inner row is still bunodont, is pretty conclusive. This singular combination of cusp characters is also exhibited by *Titanotherium*, *Palæosyops*, etc. Other series of ungulates show the almost synchronous development of the crescent-shaped cusps in both outer and inner rows, but earlier forms seem to indicate pretty unanimously that the outer or buccal series are the first to be differentiated. In *Coryphodon*, figured by Cope,[1] is exhibited the inward flexure and flattening of the exterior rows of cusps of the upper molars, in a perhaps unparalleled degree.

The change of view is simply in regard to the manner in which the modifying force is applied, and does not change the principle involved, which assumes broadly that the lateral mandibular movements produce lateral changes in dental forms, whilst on the other hand reciprocating ones produce antero-posterior and postero-anterior ones. Having definitely concluded as to the direction of the action of the forces, in evidence of which a great catalogue of facts might be adduced, more indeed than my space and means will afford, I will briefly consider that offered by the molar dentition of *Symborodon.*

In the diagram[2] which represents a rear molar of the right side seen from in front, in which E is the external and I the internal side; the simple anterior inner bunodont cusp B is seen to be but little modified, whilst the outer selenodont cusp S is seen to be much worn away, showing great disparity of development between the two. The appearance of tubercle S in vertical median transverse section, is indicated by the entire and dotted lines from *a* to *a′*

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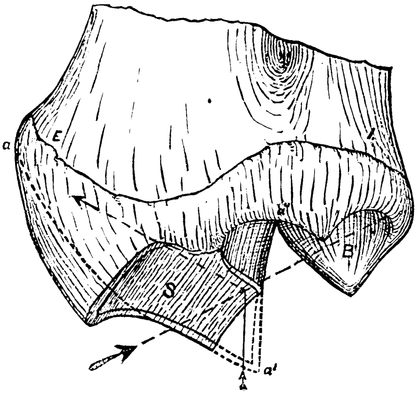
[1] U. S. Geog. Surveys West of the 100th Meridian, Vol. IV. Vertebrate Palæontology, 4to., by E. D. Cope. Washington, 1877.

[2] Prof. Cope has permitted me to make this sketch from a specimen in his superb collection of remains of these extinct animals.



and a'', the apical portion worn off being restored in outline. This shows that S has been deflected in an inward direction, and indicates that the force operative in causing the deflection has been constantly active from one side, or that upon which the large arrow is placed pointing in the direction of the dotted line. The total displacing force exerted by the jaw moving in an inward direction during the entire lifetime of the animal may be supposed to be represented by this arrow, plus that of its ancestry, during the existence of which the tooth has been brought to its present form by the mechanical process of differentiation indicated. The muscular power or crushing force exerted by the mandibular muscles (the coefficient of which is 104 pounds per square inch of section, *Haughton*) in an upward direction indicated by the lower smaller arrow pointing upwards in the direction of the entire vertical line, would tend while the mandible is moving inwards and obliquely upwards to act as a wedge upon the somewhat oblique faces of the upper molars, forcing them outwards in the direction of the dotted line and arrow pointing towards *a*. In this way the cause of the anisognathism is accounted for, whilst it is also not to be forgotten, that the influence of this peculiar combination of forces cannot be without effect in producing modifications upon the crowns of the teeth from within, so that in reality, modifying forces may be at work from both sides.